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Using novel spawning ground indices to analyze the effects of climate change on Pacific saury abundance

Shigang Liu[a], Yang Liu[a], Caihong Fu[b], Luxin Yan[a], Yi Xu[b], Rong Wan[c], Jianchao Li[a], Yongjun Tian[a,d,*]

[a] Fisheries College, Ocean University of China, Qingdao, China
[b] Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, Canada
[c] National Engineering Research Center for Oceanic Fisheries, Shanghai Ocean University, Shanghai, China
[d] Laboratory for Marine Fisheries Science and Food Production Processes, Pilot National Laboratory for Marine Science and Technology, Qingdao, China

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A B S T R A C T

Pacific saury (*Cololabis saira*) are widely distributed in northwestern Pacific, migrating from their spawning ground in subtropical Kuroshio waters south of Japan to feeding grounds in Oyashio waters northeast of Japan. The abundance of Pacific saury is expected to be affected not only by environmental conditions in the fishing grounds of the Oyashio region, but also by recruitment processes influenced by environmental conditions in the Kuroshio region. In this study, we focus on the effects of environmental variations in the spawning ground on Pacific saury abundance, approximated by catch and catch per unit effort (CPUE) data. To examine interannual-decadal variability in the spawning ground, we developed a suite of spawning ground indices, including (1) average winter sea surface temperature (WSST), (2) the meridional position of 19 °C sea surface temperature (SST) isoline (MP19), and (3) SST-suitability-weighted size of spawning ground (WSSG), in the Kuroshio region. These spawning ground indices exhibited interannual-decadal variation patterns with regime shifts in 1962/63, 1976/77, 1987/88, 1997/98, and likely in the early 2010s, which corresponded well to data on catch and CPUE of Pacific saury. Large scale climatic indices such as Southern Oscillation Index (SOI) and Asian Monsoon Index (MOI) were negatively correlated with winter SST in most of the Kuroshio region, suggesting that large-scale climatic influences played important roles in the variability of SST within the Kuroshio region. Gradient forest analyses were used to quantify the importance of these spawning ground indices for explaining the variations of Pacific saury abundance and to identify shifts in catch and CPUE along the gradients of the spawning ground indices. MP19 with a 2-year lag (MP19_Lag2) was identified as the most important predictor of Pacific saury abundance in terms of CPUE, followed by WSST_Lag2, WSST, WSSG_Lag1, and WSSG. Spawning ground indices, particularly MP19_Lag2, were useful for rationalizing the dynamics of Pacific saury abundance, matching well the striking declines of catch both in the early 1960s and also in the most recent years.

1. Introduction

Pacific saury (*Cololabis saira*) is one of the most commercially important small pelagic species in Asian-Pacific countries, especially Japan, having a wide distribution throughout the middle latitudes of the North Pacific (Watanabe et al., 1988; Zhang and Gong, 2005; Huang et al., 2007). The lifespan of Pacific saury is 2 years, with sexual maturity being reached in about 280 days, at a point where growth had approximately 28 cm in knob length (Nakaya et al., 2010). The spawning season of Pacific saury lasts from September to June, with a peaking in winter, with individual fish spawning several times during the single extended spawning season (Kosaka, 2000; Suyama, 2002; Watanabe et al., 2003).

As an intermediate-trophic-level species, Pacific saury plays an important role in the pelagic ecosystem, both as a predator on zooplankton and as a prey for large predatory fish in northwestern Pacific Ocean (NWP) (Oozeki et al., 2015). Pacific saury migrates from Oyashio water to Kuroshio water through the Kuroshio–Oyashio transition zone of complex oceanic structures (Fig. 1) (Watanabe et al., 1988, 1997). The migration of Pacific saury is considered to be driven both by the requirement for suitable water temperatures for spawning as well as by the need to achieve optimal access to food resources (Huang and Huang, 2015; Sugisaki and Kurita, 2004).

Japan was the first country to utilize Pacific saury resources, achieving the largest catches of this species in the world during the last

* Corresponding author at: Ocean University of China, Yushan Road 5, Qingdao, China.
E-mail address: yjtian@ouc.edu.cn (Y. Tian).

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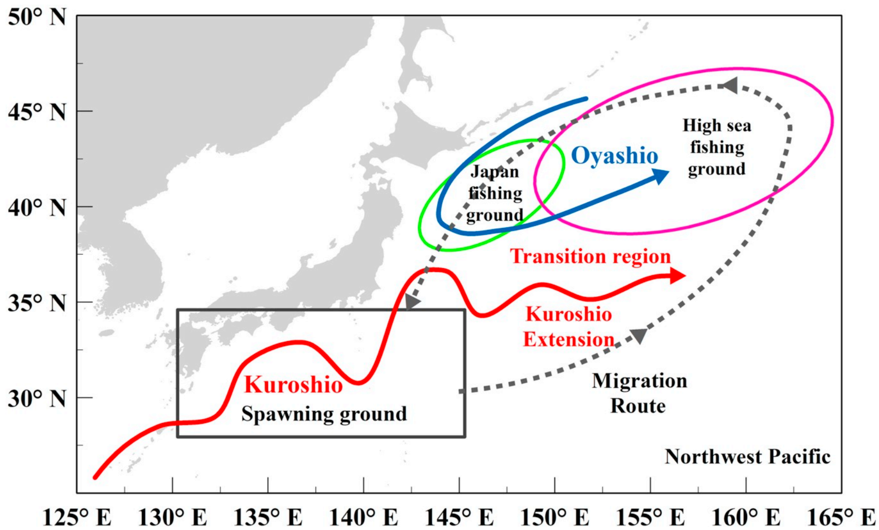

Fig. 1. Schematic diagram showing the spawning ground and migration route of Pacific saury with the oceanographic structures along the Pacific coast of Japan. The solid red line represents the Kuroshio Current and Kuroshio Extension, while the solid blue line represents the Oyashio Current. The dotted line with arrows represents the migration route of Pacific saury. The black box indicates the Kuroshio region, a main spawning area of Pacific saury in winter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

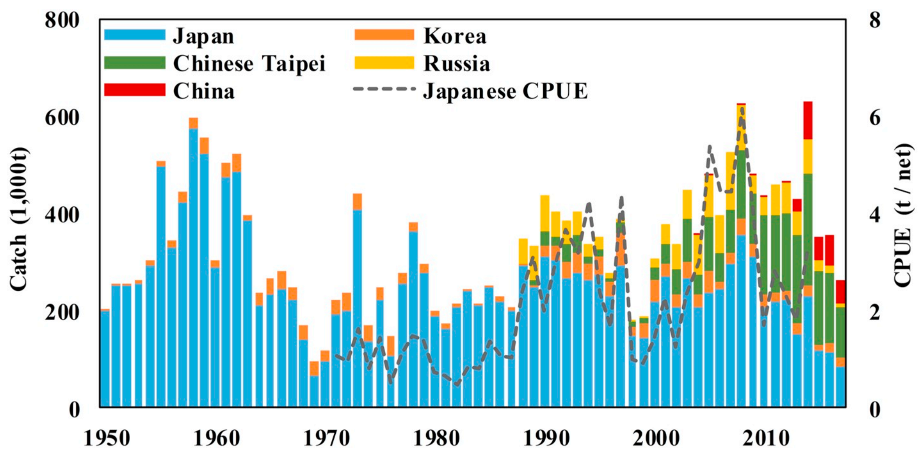

Fig. 2. Annual catch and CPUE of Pacific saury by country and region from 1950 to 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

century. Japan maintains long time series of catch per unit effort (CPUE) data (tons per net), which show similar annual variations with catch (Fig. 2). Annual catch of Pacific saury by Japan fluctuated by an order of magnitude from 572,000 t in 1958 to 63,000 t in 1969, with large declines during 1960s and during very recent years. Korea started fishing Pacific saury at an early time, but catch has always remained at a relatively low level. Russia and Chinese Taipei began fishing Pacific saury in the late 1980s, with their catches rapidly increasing after 2000. China enhanced the fishing efforts on Pacific saury after 2013 resulting in drastically increased catch. Japanese fishing vessels mainly operate in the Japanese exclusive economic zone (EEZ) along the Japanese northeast coast, while China and Taiwan vessels mostly catch Pacific saury in the high seas fishing grounds to the east of the Japanese and Russian EEZs (Fig. 1) (Huang et al., 2007). The main fishing season is in autumn when Pacific saury migrates southward (Suyama, 2002; Huang, 2010).

In recent years, total catch of Pacific saury throughout the entire region has declined greatly. In particular, the Japanese catch dropped from 354,727 t in 2008 to 84,528 t in 2017, which is the lowest catch since 1968 (Fig. 2). The fisheries management issues and stock assessments of Pacific saury have been respectively discussed and executed under the auspices of the North Pacific Fisheries Commission (NPFC) since it was established in 2015. In order to better predict the abundance of Pacific saury, and to thereby effectively manage the resource, the controlling mechanisms underlying the population dynamics need to be more clearly elucidated.

A large number of studies of oceanic conditions in the "downstream" Oyashio waters have demonstrated that the migratory pattern and fishing grounds of Pacific saury are clearly associated with environmental conditions such as sea surface temperature (SST), chlorophyll-*a* concentration and ocean current in Oyashio water (e.g., Yasuda and Watanabe, 1994; Tseng et al., 2011, 2014; Kuroda and Yokouchi, 2017). However, a few recent studies have suggested that the abundance of Pacific saury was affected not only by the environmental conditions in the fishing and feeding grounds, but also by the recruitment process in the spawning ground in the "upstream" subtropical Kuroshio waters (Zhang and Gong, 2005; Yasuda and Watanabe, 2007; Oozeki et al., 2015; Ichii et al., 2018). In particular, SST data in the Kuroshio region during winter was closely related to the spatial distribution and potentially the survival of Pacific saury, although they were not able to fully explain the environmental effects on the abundance of Pacific saury (Iwahashi et al., 2006; Takasuka et al., 2014; Oozeki et al., 2015).

There is ever increasing evidence that large-scale climatic changes affect marine ecosystems by altering the local oceanographic environment (Overland et al., 2010; Tian et al., 2012, 2013; Cheung et al., 2015). It has been shown that the abundance of short-lived small pelagic species such as sardine, anchovy, squid, and Pacific saury appeared to be more affected by oceanic and climatic factors than by fishing (Chavez et al., 2003; Tian, 2009; Ma et al., 2018). Previous studies on the recruitment and abundance of Pacific saury highlighted the importance of climate-induced environmental variabilities in

subtropical Kuroshio waters (Tian et al., 2003, 2004; Zhang and Gong, 2005; Ichii et al., 2011). However, they failed to explain the dramatic decline of catch in the early 1960s, which was the most significant change after 1950. Essentially, the mechanism for climate-induced variations in SST and their ecological consequences on Pacific saury dynamics has not been well understood.

Because Pacific saury tend to actively select a suitable SST to spawn (Takasuka et al., 2014), optimal position and effective size of spawning ground may change according to the distribution of winter SST in the Kuroshio region, with possible vital effects on spawning and recruitment of Pacific saury. Therefore, we used the average winter SST (WSST) in the Kuroshio region as an index of Pacific saury spawning ground conditions. In addition, we developed two novel spawning ground indices, the meridional position of the 19 °C SST isoline (MP19) and the SST-suitability-weighted size of potential spawning ground (WSSG) in the Kuroshio region. The objectives of the research are (1) to evaluate the effects of climate change on the winter spawning ground conditions as reflected in the spawning ground indices, (2) to quantify the relationships between spawning ground indices and Pacific saury abundance approximated by catch and CPUE of Pacific saury, (3) to elucidate the possible controlling mechanism for climate-induced variability in the abundance of Pacific saury, and (4) to attempt to explain the decline of catch both in the early 1960s and in the most recent years.

2. Materials and methods

2.1. Fishery data

Japan has the longest history of fishing Pacific saury with catch prior to the 2010s having been much higher than those by other countries (Fig. 2). Meanwhile, only Japan has assembled long time series of CPUE data (Fig. 2). In this study, we used the Japanese catch and CPUE data to represent the abundance of Pacific saury. The Japanese catch data for the earlier period of 1950–2014 were obtained from FAO (FAO, 2016) and those for the later period of 2015–2017 were from NPFC (https://www.npfc.int/summary-footprint-pacific-saury-fisheries). Annual Japanese CPUE data for the period of 1971 to 1980 were obtained from Tian et al. (2004) and those for the period of 1980 to 2014 were from the Annual Research Report of Pacific saury by Fisheries Agency of Japan (Tohoku National Fisheries Research Institute, Fisheries Research Agency, 2015).

2.2. SST data

Monthly SST data between 0°–60°N and 120°–180°E from 1950 to 2018 were gathered from three different sources due to the lack of a data set covering the entire time period. Monthly SST for the period of 1950 to 2011 with a resolution of 1° (latitude × longitude) was obtained from the archived data set of Japan Meteorological Agency (JMA) (http://www.jma.go.jp/jma/index.html). Monthly SST for the period of 1985 to 2016 were derived from Advanced Very High Resolution Radiometer (AVHRR) with a resolution of 9 km and those for the period of 2013 to April 2018 were derived from Geostationary Operational Environmental Satellites (GOES) with a resolution of 4 km (http://oceanwatch.pifsc.noaa.gov/thredds/catalog.html). To ensure data consistency in spatial resolution, we transformed the AVHRR and GOES data into the resolution of 1° (latitude × longitude) by using the method of arithmetic mean. Then, we used the JMA data to cover the period of 1950 to 2011, the AVHRR data to cover 2012 to 2016 and the GOES data for 2017 to 2018.

2.3. Climatic indices

Southern Oscillation Index (SOI), Asian Monsoon Index (MOI), Pacific Decadal Oscillation (PDO) and Arctic Oscillation Index (AOI) data were chosen as appropriate climatic indices for the NWP. These climatic indices are well documented and closely associated with variabilities in the NWP ecosystem (Overland et al., 2008; Tian et al., 2008). Monthly SOI, PDO and AOI were derived from the National Centers for Environmental Information, NOAA (https://www.ncdc.noaa.gov/teleconnections/). MOI data were updated from Tian et al. (2013). All climate indices cover the period of 1950 to 2018 except that the SOI lacks the data for 2018. Annual SOI (up to 2017) is defined as the average over May to next April, which has significant correlations with winter SST in the NWP (Tian et al., 2003). The winter PDO, MOI, AOI indices are the average over the previous December to February, a period with the most significant climate variability in the NWP (Overland et al., 2008).

2.4. Estimated spawning ground indices

We estimated WSST as the average SST from January to March, which are the coldest months in the NWP and comprise the winter spawning period of Pacific saury (Tian et al., 2003). In addition to WSST used as a spawning ground index, we developed two new indices, the meridional position of 19 °C SST isoline and SST-suitability-weighted size of potential spawning ground in the Kuroshio region, as spawning ground indices to analyze the effects of spatial dynamics of winter SST on Pacific saury. We defined the Kuroshio region as being the area of 28–35°N, 130–145°E (Fig. 1), covering the winter spawning ground of Pacific saury (Tian et al., 2004;Takasuka et al., 2014). SST has been found to be the most important factor for spawning and larval survival of Pacific saury, with suitable spawning SST ranging from 16 to 22 °C and an optimal SST at 19 °C (Watanabe et al., 1997; Iwahashi et al., 2006; Takasuka et al., 2014). Therefore, we employed the average latitude of 19 °C SST isoline between 130 and 145°E (MP19) to describe the meridional variations of optimal spawning ground.

Previous studies used the sum of suitable SST range as the size of spawning ground (Sakurai et al., 2000; Rosa et al., 2011; Yu et al., 2018). However, these studies have not considered the differential effects of SST variability on the spawning and survival rate of Pacific saury in the estimation of spawning ground size. To account for the effects of SST variability, we developed a novel WSSG index to define the effective area of spawning ground through weighting by a temperature suitability index (TSI), i.e., the probability of spawning at a specific SST. Based on the suitable and optimal spawning SST mentioned above, we assume TSI at SST t (TSI_t) to be normally distributed as:

$$TSI_t = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(t-\mu)^2}{2\sigma^2}} \tag{1}$$

where μ is the mean SST = 19 °C, σ is the variance = 1.5 with approximately 95% of the area being within 16 to 22 °C. The WSSG in year i is calculated as:

$$WSSG_i = \sum_{j=1}^{N_i} S_j \times TSI_j \tag{2}$$

where N_i is the number of grids with SST between 16 and 22 °C in the Kuroshio region in year i, TSI_j is the TSI of grid j, and S_j is the size of grid j fixed at 1 × 1° (latitude × longitude).

2.5. Data analyses

Correlation analyses combined with significance tests were used to examine the relationships among climatic indices and spawning ground indices. In order to further investigate the correlation field between SST and climatic indices, the horizontal distribution of correlation coefficients between the climatic indices and the winter SST in NWP was mapped. The correlation coefficient of each point with 1-degree (latitude × longitude) resolution was calculated by the correlation analysis

between the winter SST at this point and the various climatic indices for the period of 1950 to 2018. As SOI has a lagged effect on SST in the Kuroshio region, the correlation analysis between SOI and other indices used the 1-year lagged SST data (Tian et al., 2002) for the period of 1951 to 2017.

Sequential *t*-test analyses of regime shifts (STARS; Rodionov, 2004) were applied to detect trends and step changes within the time series data. STARS results are determined by the significance level, cut-off length for proposed regimes and the Huber's weight parameter, which defines the degree of departure from the observed mean beyond which observations are considered as outliers. In this study, the STARS cut-off length was consistently set to 10, Huber's weight parameter to 1 and significance level to 0.1. In the STARS analyses, the temporal periods for catch and CPUE data were from 1950 to 2017 and from 1971 to 2014, respectively. In order to show more clearly the variations in catch after 1964, the catch data after 1964 was analyzed independently. Climatic indices for the period of 1950 to 2018 were used in the STARS analyses, except that the period for the SOI was from 1950 to 2017. We also used the cumulative sum (CuSum) of the anomalies from the time series data to examine the trend in all indices. The method of CuSum is a simple addition of a datum to the sum of all previous data points, and the CuSum graph makes the trend in a time series more intuitive (Beamish et al., 1999). Anomalies were calculated by dividing each data point by the mean of the entire time series.

In order to further quantify the relationships between the spawning ground indices and the catch and CPUE of Pacific saury, we employed a machine learning approach: gradient forests (R package gradient Forest, R Core Team, 2017). Gradient forest method was built upon random forests to capture complex relationships between potentially correlated predictors and multiple response variables by integrating individual random forest analyses over the different response variables (Ellis et al., 2012). In essence, random forests are regression trees that partition the response variable into two groups at a specific split value for each predictor p to maximize homogeneity. An independent bootstrap sample of data is used to fit each tree and the data not selected in the bootstrap sample (i.e., out-of-bag OOB data) are used to provide a cross-validated estimate of the generalization error. Along with other measures, gradient forests provide the good-of-fit R_f^2 for each response variable f, the accuracy importance I_{fp} for a predictor p, and the importance weighted by R_f^2. Accuracy importance I_{fp} is the increase in OOB mean square prediction error when the predictor p is randomly permuted with large values indicating the predictor has true predictive power which is eroded when the predictor is permuted (Ellis et al., 2012). The importance of a split value along a predictor gradient reflects the relative change in the response variable. We ran the gradient forests 1000 times to obtain the mean and standard deviation (*sd*) of R_f^2. The run with the highest overall performance (R^2) was then used to derive I_{fp} and other statistics.

3. Results

3.1. Variations in catch and CPUE

The Japanese catch and CPUE of Pacific saury had similar annual variations with a correlation of r = 0.52, $p < 0.01$. Decadal variations in Japanese catch and CPUE were estimated by STARS. Japanese catch showed significant regime shifts in 1963/64 and 2014/15 (Fig. 3A). The dramatic regime shift in 1963/64 overshadowed the post-1964 catch variations. Therefore, we estimated the regime shifts in catch data after 1964 independently (Fig. 3B). After 1964, catch showed regime shifts in 1976/77, 1987/88, 1997/98, and 2012/13. CPUE showed regime shifts in 1987/88, 2004/05, and 2009/10 (Fig. 3C).

3.2. Variations in spawning ground indices

The interannual variations in WSST in the Kuroshio region showed an increasing trend especially during 1970 to 2007 (Fig. 4A). The variations in MP19 were similar to those in WSST (r = 0.94, $p < 0.001$). The southernmost MP19 reached 29.5°N in 1968 and the northernmost reached 33.4°N in 2007 (Fig. 4B). The 5-year moving averages in WSST and MP19 showed approximately 10-year cyclical fluctuations after 1976. Conversely, the interannual variations in WSSG showed a declining trend with maximum WSSG in 1951 and minimum in 1999 (Fig. 4C), respectively, while WSSG showed no significant correlations with WSST and MP19.

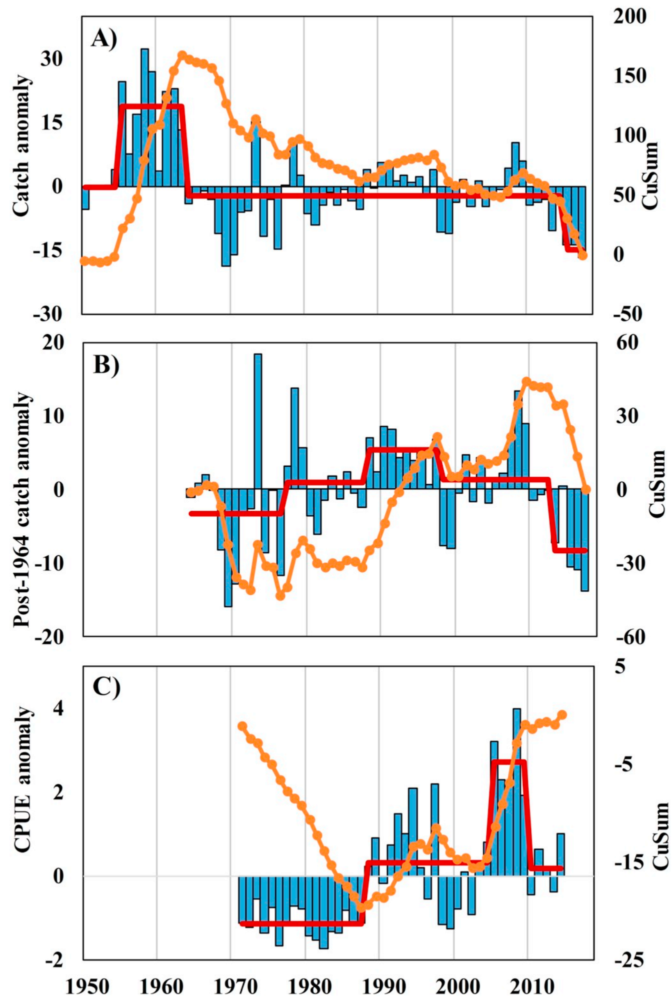

Fig. 3. Annual anomalies (blue bars) for A) Japanese catch, B) Japanese catch after 1964, and C) Japanese CPUE of Pacific saury with orange lines showing cumulative sum (CuSum) of anomalies and red lines representing regime shifts detected by STARS. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Decadal variations in the three spawning ground indices were estimated by STARS. WSST in the Kuroshio region showed regime shifts in 1987/88 and 2010/11 (Fig. 4D). MP19 displayed regime shifts in 1962/63, 1977/78, 1987/88 and 2010/11 (Fig. 4E), while WSSG showed regime shifts in 1961/62, 1996/97, 2014/15 (Fig. 4F). Higher WSSG was often accompanied by medium MP19 such as in 1958 (Fig. 5A), and lower WSSG was associated with abnormal MP19 such as in 1999 (Fig. 5B). The decadal distribution of southernmost 19 °C SST isolines reached 30°N in the period 1963–1977 and northernmost reached 34°N in 2011–2018 (approximately). The average MP19 during the period of 2011–2018 was lower than that during 1988–2011. However, the average 19 °C SST isoline was the highest between 130 and 139°E compared to the other four periods. The decreased MP19 during the period of 2011–2018 was affected by the meander of the 19 °C SST isoline around 140°E. In general, the 19 °C SST isolines

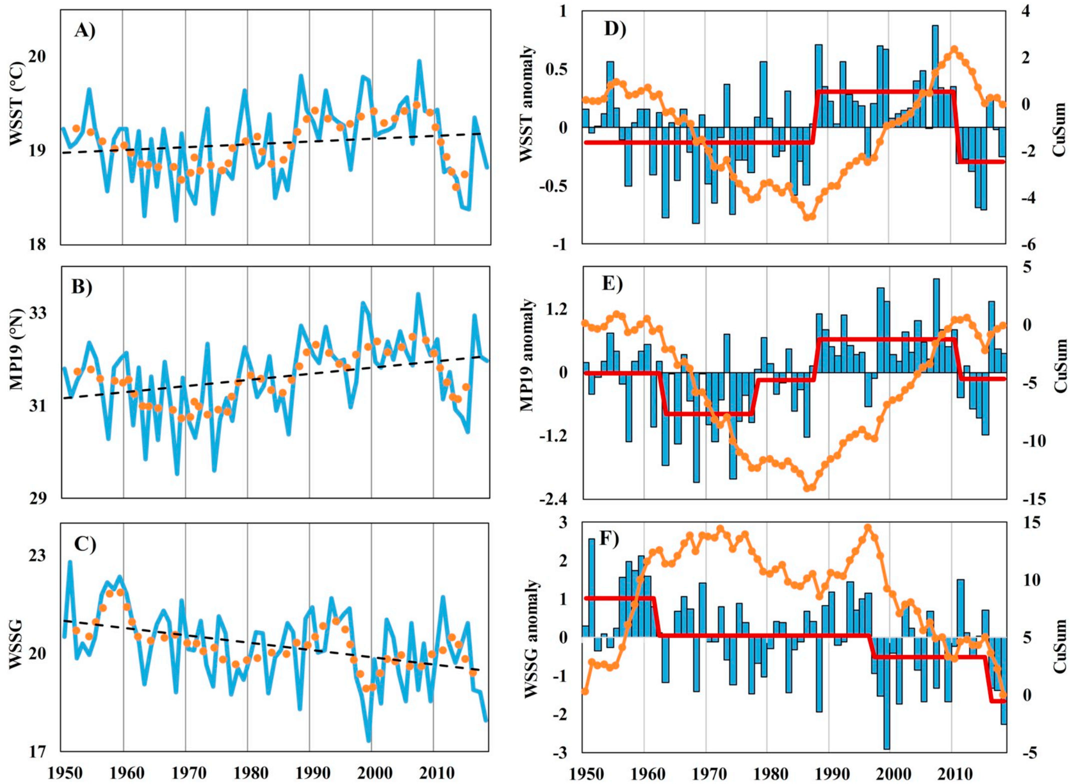

Fig. 4. Annual variations (solid blue lines) and anomalies (blue bars) of average winter SST in the Kuroshio region (WSST, A and D), the meridional position of 19 °C SST isoline (MP19, B and E), and SST-weighted size of spawning ground (WSSG, C and F) during 1950 to 2018. The dotted orange lines and dashed black lines in panels A to C represent 5-year moving averages and linear trends, respectively. The orange lines and red lines in panels D to F represent cumulative sum (CuSum) of anomalies and STARS-detected regime shifts, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

showed significant decadal variations, particular between 135 and 140°E, with continuous northward movement after the shift in 1977/78 (Fig. 6).

3.3. Climate-induced variations in winter SST

The climatic indices showed evident decadal variability for the period of 1950 to 2018 with regime shifts in 1976/77 and 1988/89 for PDO, in 1976/77 and 1998/99 for SOI, a regime shift in 1988/89 for AOI, and regime shifts in 1986/87 and 2004/05 for MOI (Fig. S1). There are some regime shift overlaps among these four climatic indices. In the Kuroshio region, no correlation was found between winter PDO and winter SST (Fig. 7A) and marginal positive correlations were present between winter AOI and winter SST (Fig. 7C). On the other hand, both annual SOI and winter MOI showed negative correlations with winter SST in most of the grids within the Kuroshio region (Fig. 7B and

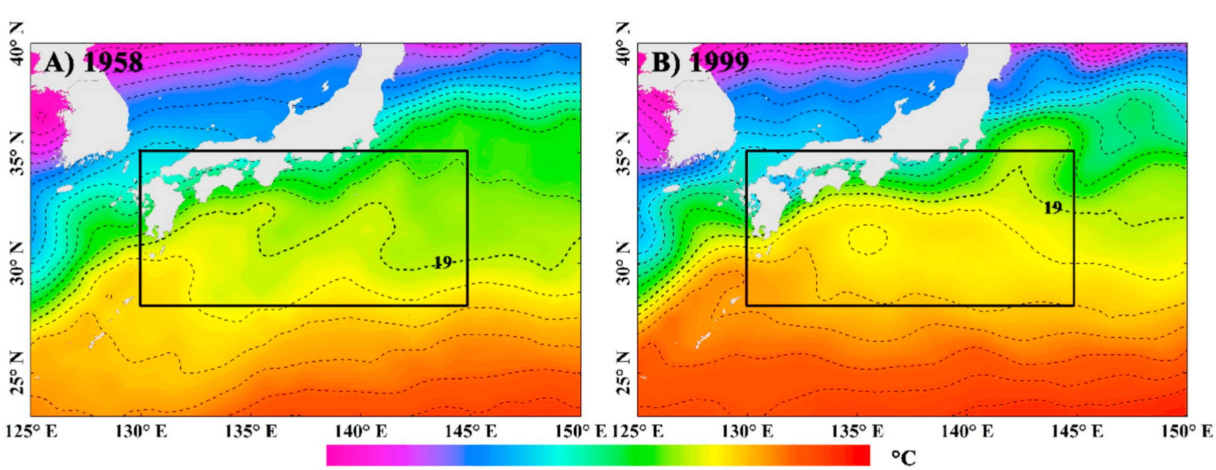

Fig. 5. The distribution of winter SST in 1958 with higher WSSG (A) and in 1999 with lower WSSG (B), respectively. The dashed lines are SST isolines with 1 °C intervals and the black box indicates the Kuroshio region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

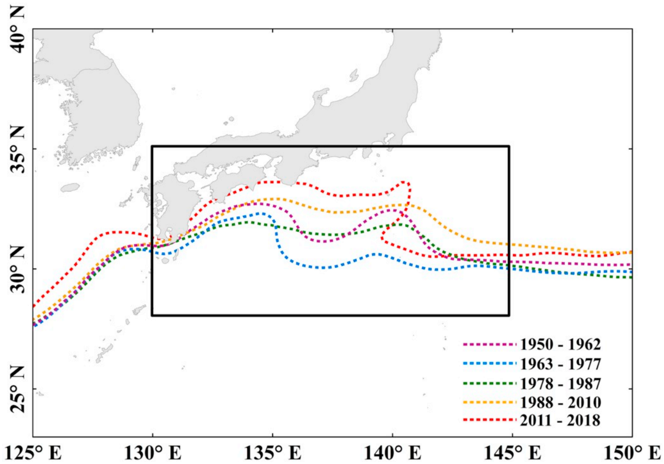

Fig. 6. The decadal distribution of average winter 19 °C SST isolines during 1950 to 2018. The black box indicates the Kuroshio region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

D). For annual SOI and winter MOI, significant negative correlations were also found with MP19 (Table 1). These results indicated that the mechanisms underlying annual SOI and winter MOI played important roles in determining winter SST dynamics in the subtropical Kuroshio waters.

3.4. Gradient forest analyses

Initial gradient forest analyses were carried out to explore the responses of catch and CPUE to all climatic indices (i.e., PDO, SOI, AOI, and MOI) and spawning ground indices (i.e., WSST, MP19, and WSSG) along with their 1- and 2-year lagged time series. However, all of the climatic indices and their lagged time series showed negligible importance as predictors while spawning ground indices and their lagged time series constituted the seven most important predictors (results not shown). Therefore, the climatic indices were excluded from the following gradient forest analyses in order to achieve better model performance.

Based on 1000 runs of gradient forests, the performance (goodness-of-fit R_f^2) for catch (mean = 0.053, sd = 0.015) was significantly lower than that for CPUE (mean = 0.113, sd = 0.017), indicating spawning ground indices can predict CPUE better than they can predict catch (Fig. 8), agreeing with the fact that CPUE is the more effective indicator of Pacific saury abundance. Out of the 1000 runs, the best one with the highest overall performance R^2 was used to quantify the relationships between spawning ground indices and Pacific saury abundance.

The gradient forest model identified MP19 with a 2-year lag (MP19_Lag2) as the most important predictor with the highest mean

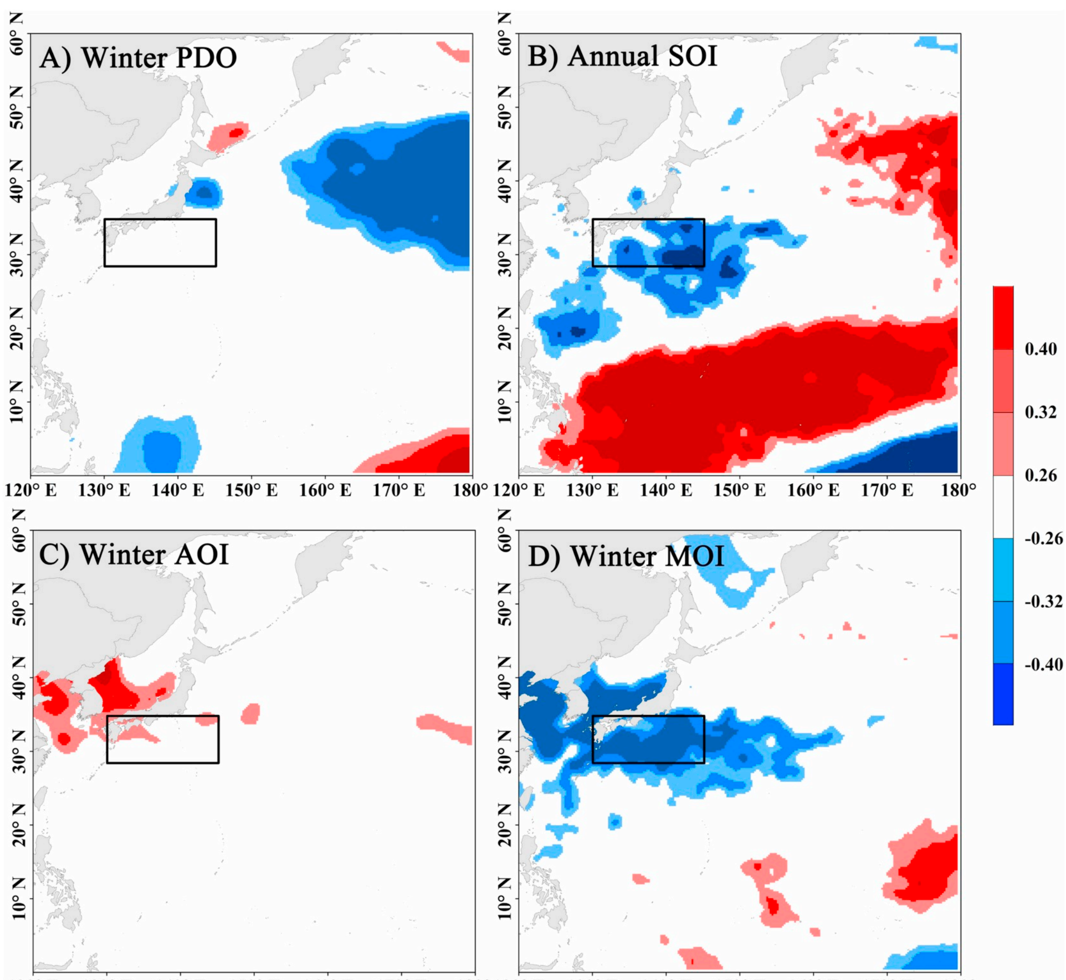

Fig. 7. Maps of correlation between winter SST and climatic indices: A) winter Pacific Decadal Oscillation (PDO), B) annual Southern Oscillation Index (SOI), C) winter Arctic Oscillation Index (AOI), and D) winter Asian Monsoon Index (MOI) during 1950 to 2018. The correlation map for annual SOI used 1-year lagged winter SST data. The correlation coefficients of 0.26, 0.32 and 0.40 correspond to the statistical significance levels of 0.05, 0.01 and 0.001, respectively. The black boxes indicate the Kuroshio region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Correlations among spawning ground indices and climatic indices. The bold represent significant correlations. Single and double asterisks represent significance at $p < 0.05$ and $p < 0.01$, respectively. WSST: the average winter SST in the Kuroshio region, MP19: the meridional position of 19 °C SST isoline, WSSG: SST-weighted size of spawning ground, PDO: Pacific Decadal Oscillation, SOI: Southern Oscillation Index, AOI: Arctic Oscillation Index, MOI Asian Monsoon Index.

	WSST	MP19	WSSG	Winter PDO	Annual SOI	Winter AOI
MP19	**0.94****	–				
WSSG	−0.22	−0.22	–			
Winter PDO	−0.03	0.02	0.10	–		
Annual SOI	**−0.41****	**−0.4****	−0.1	**−0.54****	–	
Winter AOI	0.22	**0.27***	0.17	**−0.28***	0.07	–
Winter MOI	**−0.58****	**−0.55****	−0.01	−0.06	**0.33***	**−0.35****

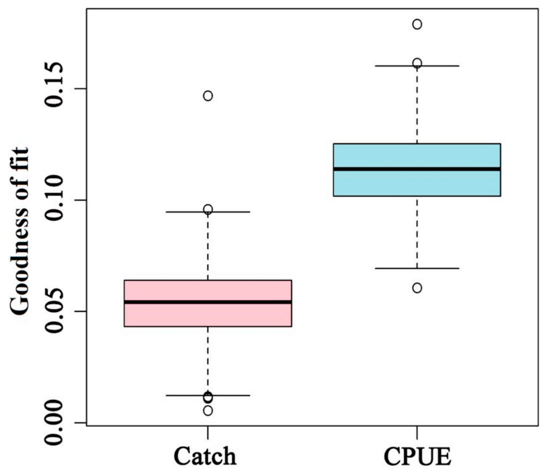

Fig. 8. Model performance (goodness-of-fit R^2) of 1000 runs of the gradient forests for catch and CPUE.

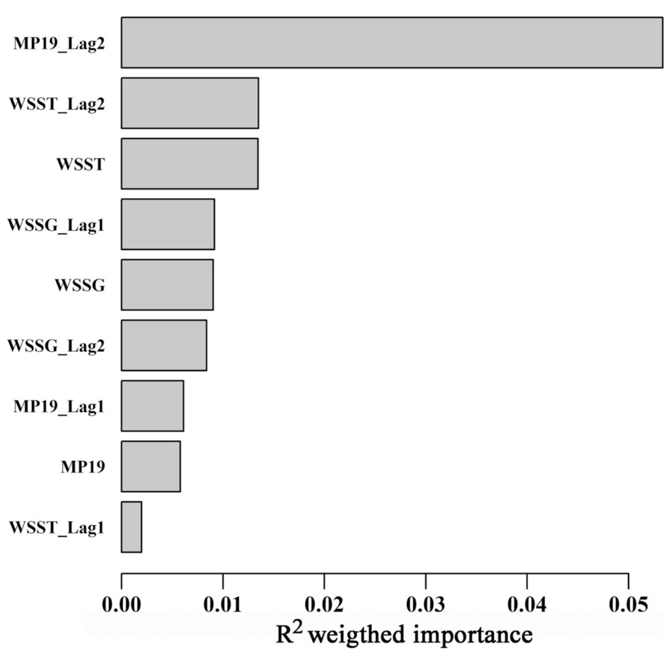

Fig. 9. Importance of spawning ground indices (MP19: the meridional position of SST 19 °C isoline, WSST: the average winter SST in the Kuroshio region, and WSSG: SST-weighted size of spawning ground) and their 1- (with suffix "_Lag1") and 2-year (with suffix "_Lag2") lagged time series across catch and CPUE outputs (R^2) from the gradient forest analyses.

importance, as measured by its contribution to prediction accuracy on the OOB samples, followed by WSST_Lag2, WSST, WSSG_Lag1, and WSSG (Fig. 9). In comparison, MP19_Lag1, MP19, and WSST_Lag1 were the least important predictors, and so were excluded from the cumulative important plots. CPUE of Pacific saury had a strong threshold response when MP19_Lag2 was around 31.5 to 32°N, whereas catch was not sensitive to the changes in MP19_Lag2 (Fig. 10A). In addition, CPUE was responsive to WSST_Lag2 and WSST when these predictors were > 19 °C (Fig. 10B, C). On the other hand, catch had strong threshold responses to WSSG-related but less important predictors (i.e., WSSG_Lag1, WSSG, and WSSG_Lag2) between 21.5 and 22 (Fig. 10D–F).

4. Discussion

4.1. The effects of WSST on Pacific saury

The spawning period of Pacific saury lasted from autumn to spring. However, the winter spawning cohort in the Kuroshio region was considered the most important one based on its having the highest proportion of mature adults and highest spawning density (Watanabe and Lo, 1989; Ichii et al., 2018). Many factors may affect the spawning of Pacific saury, such as ocean current, chlorophyll-*a* concentration and mixed layer depth; SST, having vital effects on mortality and growth rates in early life stages, was however considered to be the most important one (Tian et al., 2002; Watanabe et al., 1997; Tseng et al., 2011, 2014). Although monthly SST data were obtained from three sources for three consecutive periods (JMA data for 1950 to 2011, AVHRR data for 2012 to 2016 and GOES data for 2017 to 2018), the overlapped time-series among the three data sets revealed sufficient data consistency and negligible impacts on the calculations of the spawning ground indices (Fig. S2). The abundance of the large-sized group of Pacific saury showed a good correspondence with annual SST in the Kuroshio region on both interannual and decadal scales, with synchronous regime shifts occurring in 1963/64, 1976/77 and 1987/88 (Tian et al., 2003). The CPUE of age-1 Pacific saury was positively correlated with previous year's WSST in the Kuroshio region during 1979 to 2006 excluding 1994–2002 (Ichii et al., 2018). In this study, WSST in the Kuroshio region showed synchronous increase or decrease (i.e., regime shifts) with catch and CPUE of Pacific saury in 1987/88 and the early 2010s (Figs. 3 and 4D), and CPUE was responsive to changes in both 2-year lagged WSST and WSST without time lag (Fig. 10B, C), which confirmed the viewpoints of other researchers (Tian et al., 2004; Ichii et al., 2018). However, other regime shifts in catch and CPUE data aside from the two previously mentioned were not detected in WSST (Fig. 4D), indicating the variations in WSST could not completely explain the variations in Pacific saury abundance.

4.2. The effects of MP19 on Pacific saury

MP19 was estimated based on the meridional position of 19 °C SST isoline to reflect the optimal position of the winter spawning ground of Pacific saury. The gradient forest analyses identified MP19_Lag2 as the most important predictor with a far greater importance than all other predictors (Fig. 9). The 2-year delayed effects of MP19 on the abundance of Pacific saury are reasonable in that Pacific saury have a 2-year

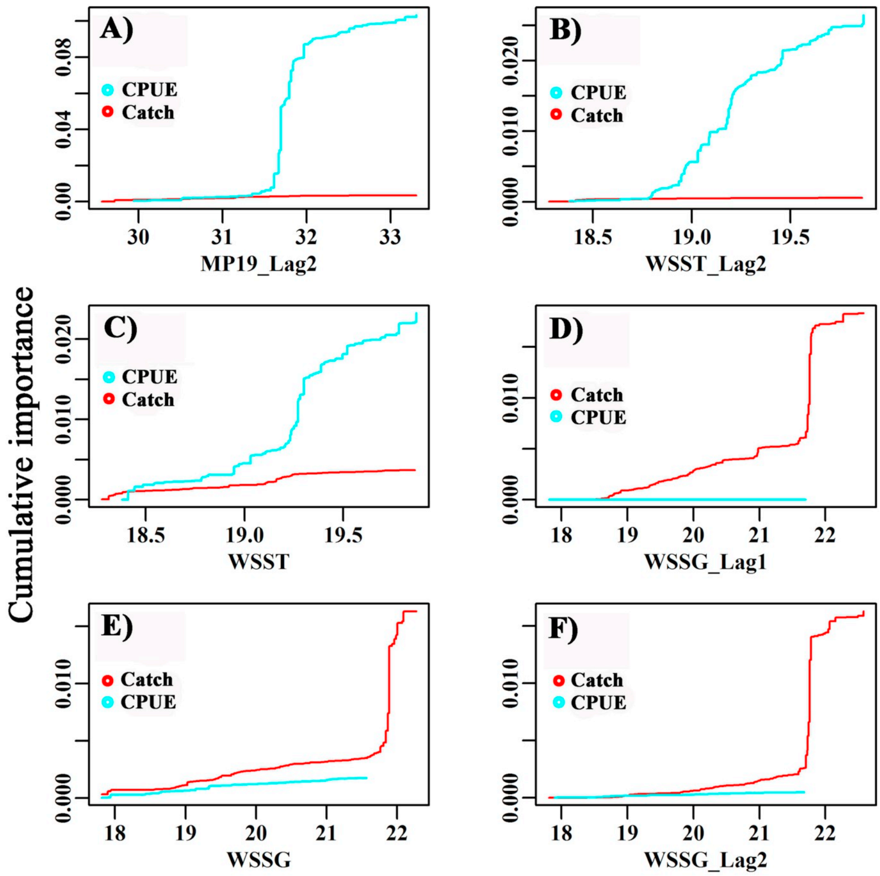

Fig. 10. Cumulative shifts (in R^2 units) of catch and CPUE in response to the first six important oceanographic variables related to spawning ground indices (MP19: the meridional position of SST 19 °C isoline, WSST: the average winter SST in the Kuroshio region, and WSSG: SST-weighted size of spawning ground). Suffixes "_Lag1" and "_Lag2" represent time lagged indices by 1 and 2 years, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lifespan. MP19 showed a significant positive correlation with WSST in the Kuroshio region (Table 1), suggesting that the increase of WSST produced the northward movement of SST isolines and of the corresponding optimal spawning ground of Pacific saury. The extreme southward move of MP19 may be caused by the Kuroshio meander (Kawabe, 1995). MP19 showed synchronies in decadal variations with catch and CPUE (Figs. 3 and 4E) and the synchronous regime shifts suggested that the increases in MP19 were beneficial for enhancing the abundance of Pacific saury, and vice versa. It has been shown that copepods, the main food for Pacific saury, were distributed more densely in the slope water than in the Kuroshio region (Hidaka and Nakata, 2010). Therefore, the northward move of MP19 may have increased the accessibility of zooplankton to Pacific saury and thus enhanced the recruitment of Pacific saury. MP19 also reflects the routes of Kuroshio Current (Kawabe, 1995), which have vital effects on oceanographic conditions in the Kuroshio region, thus indirectly affecting spawning ground conditions.

4.3. The effects of WSSG on Pacific saury

Based on the suitable SST range, the size of spawning ground has been estimated as a potential generator of variations in recruitment and abundance (Sakurai et al., 2000; Yu et al., 2018). It is well known that increase in spawning ground size can enhance temperature suitability and spatial availability for the spawning of Pacific saury, thus providing better environmental conditions for spawning and survival (Rosa et al., 2011). However, the differential effects of SST variability on spawning and survival rate had not been included for estimating size of spawning ground in previous studies (Sakurai et al., 2000; Rosa et al., 2011; Yu et al., 2018). Accordingly, in this study we incorporated weighting by SST suitability in the WSSG estimation.

WSSG showed synchronies in decadal variations with catch and CPUE (Figs. 3 and 4F). The synchronous regime shifts indicated that a decrease in WSSG was an unfavorable factor for the abundance of Pacific saury. Catch of Pacific saury tended to have strong threshold responses when WSSG (either with or without time lags) was around 21.5 to 22 (Fig. 10D, E, and F). However, WSSG was not significantly correlated with WSST and MP19 (Table 1) indicating that WSSG had a different variation pattern from that of WSST and MP19.

Despite the different variation patterns between WSSG and MP19, there were some associations between these two indices under extreme conditions. For instance, lower WSSG values were accompanied by extreme northward shifts of MP19 (Fig. 4B, C), such as occurred in 1988, 1999, 2007 and 2016, through compressing the area of 18–20 °C SST, i.e., the suitable spawning ground for Pacific saury (Fig. 5B). That implies that northward shifts of optimal spawning ground will provide better feeding conditions for Pacific saury, but an extreme northward shift will lead to a shrinking in spawning ground size. Therefore, the different effects on Pacific saury may depend on the interactions of variations in MP19 and WSSG. As the 19 °C SST isoline in most areas of spawning ground has been moving northwards in recent decades (Fig. 6), we postulate that the extreme northward extent of MP19 will occur more frequently in the future, resulting in more frequent occurrences of lower WSSG and lower Pacific saury abundance.

In conclusion, the three spawning ground indices uniquely reflect the different aspects of the Pacific saury spawning ground. Together, they provide a useful basis for rationalizing the recorded variations in the abundance of Pacific saury and have better tracked the dramatic decline of catch in the early 1960s, than did previous studies (Tian et al., 2004; Ichii et al., 2018).

4.4. Possible controlling mechanism of climate change on Pacific saury

In our research, we used STARS analyses to detect the decadal

Table 2
Catalogue of regime shifts found in various indices during 1950–2018 with climatic indices including winter PDO, winter AOI, annual SOI, and winter MOI; SST-related spawning ground indices including WSST, winter MP19, and winter WSSG; indices related to Pacific saury including catch and CPUE in Japan; and All for all the above indices. PDO: Pacific Decadal Oscillation, SOI: annual Southern Oscillation Index, AOI: Arctic Oscillation Index, MOI Asian Monsoon Index, WSST: the average winter SST in the Kuroshio region, MP19: the meridional position of 19 °C SST isoline and WSSG: SST-weighted size of spawning ground.

Indices		Shifts in					
		1950–1960s	1970s	1980s	1990s	2000s	2010s
Climatic indices	Winter PDO		1976/77	1988/89			2014/15
	Winter AOI			1988/89			
	Annual SOI		1976/77		1997/98		2013/14
	Winter MOI			1988/89		2003/04	
Spawning ground indices	WSST			1987/88			2010/11
	MP19	1962/63	1977/78	1987/88			2010/11
	WSSG	1961/62			1996/97		2014/15
Pacific saury	Catch	1963/64	1976/77	1987/88	1997/98		2012/13
	CPUE			1987/88		2004/05	2009/10
All			1976/77	1987/88	1997/98		Early 2010s

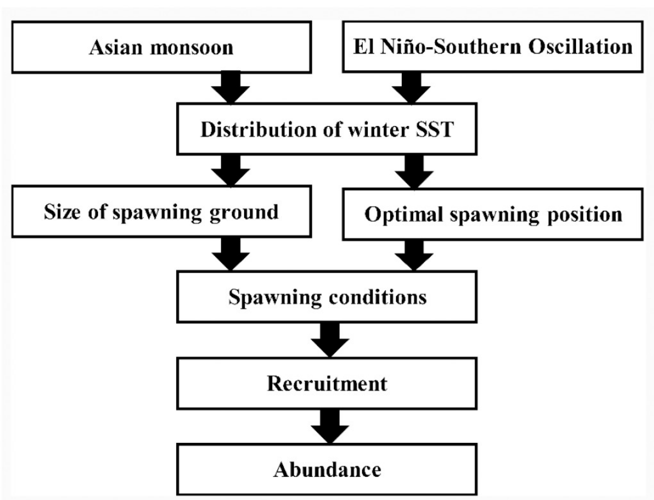

Fig. 11. Schematic diagram to show the possible processes affecting the variability of Pacific saury abundance.

variations in climatic indices, spawning ground indices, CPUE, and two time series of catch of Pacific saury (the entire time series and post-1964 time series). The fewer shift time notes in the longer catch data could be due to the higher catch around 1960, which overshadowed the variations after 1964 (Fig. 3A). By excluding the pre-1964 catch, the catch data manifested more shifts (1976/77, 1987/88, 1997/98, and 2012/13) (Fig. 3B). Focusing on the abundance of large-sized Pacific saury during 1950 to 2000, Tian et al. (2003) also showed similar shifts in 1963/64, 1976/77, 1987/88, confirming that Pacific saury has indeed changed around those years. The significant regime shifts in climatic indices were detected around 1976/77, 1988/89 and 1997/98, which were also reported by other researches (Overland et al., 2008; Tian et al., 2013). These climate regime shifts have been well recognized, indicating that the climatic regime shifts detected in our research are reliable (Fig. S1).

By summarizing all our STARS analyses, the decadal variations in climatic indices, spawning ground indices, and catch and CPUE of Pacific saury showed the same shift time nodes in 1976/77, 1987/88, 1997/98, and likely in the early 2010s (Table 2). A number of studies have concluded that changes in climate and upper ocean temperature were causes of regime shifts in the NWP marine ecosystem (Mantua and Hare, 2002; Chavez et al., 2003; Overland et al., 2008). During 1976/1977, climate-induced variations in wind-forced ocean circulation and transport resulted in a cold anomaly in the winter SST field along the subtropical North Pacific and produced an anomalous nutrient-rich water supply in the mixed layer (Parrish et al., 2000). The shift in SST is an important manifestation of climate change. In this study, AOI, SOI and MOI showed significant correlations with MP19 and winter SST in the Kuroshio region (Table 1). Correlation maps between climatic indices and winter SST indicated that MOI and SOI had strong effects on subtropical Kuroshio waters, particularly in the spawning ground of Pacific saury (Fig. 7). These results strongly indicated that large-scale climate change, especially MOI and SOI, had significant effects on the variations of winter SST in the spawning ground of Pacific saury. In particular, extreme climate events associated with Asian monsoon and with El Niño and La Niña episodes had large impact on the SST field in the spawning ground of Pacific saury, as concluded by Tian et al. (2003, 2004). However, climatic indices alone cannot explain the variations in catch and CPUE of Pacific saury, bearing negligible importance to predicting catch and CPUE based on our initial gradient forest analyses (results not shown). In contrast, the spawning ground indices developed in this study were identified as the most important predictors. In addition, the decadal variations in the spawning ground indices were well synchronized with those in catch and CPUE. It proved that Pacific saury abundance showed a good correspondence with the variations in winter spawning ground reflected by the spawning ground indices.

From the above relationships among climatic indices, SST-related spawning ground indices, and CPUE and catch of Pacific saury, we illustrate schematically the possible processes of climate change affecting the variability of Pacific saury abundance (Fig. 11). The controlling mechanism of regime shifts in the abundance of Pacific saury can be explained as follows. The climate regime shift in the Asian Monsoon and El Niño-Southern Oscillation (ENSO) events affect the WSST in the Kuroshio region, which alters the size and position of spawning ground containing optimal SST for spawning. The alteration of size and position of spawning ground changes the conditions of spawning and survival, which subsequently affects the recruitment and abundance of Pacific saury. By this mechanism, the decreased catch and CPUE in recently years can be well explained by the continuous decrease in WSST and MP19 during 2010 to 2015 and the abnormally low WSSG during 2015 to 2017. Large declines in catch in recent years also have occurred in some other small pelagic species whose winter spawning grounds are located in the waters of the Kuroshio Current (e.g., Japanese flying squid, *Todarodes pacificus*) (Kidokoro et al., 2010; Yu et al., 2018). Our study thus indicates that variations in oceanographic environment in the Kuroshio region have significant effects on the small pelagic species spawning in Kuroshio waters in winter (Sakurai et al., 2000; Yasuda et al., 2014). Therefore, it is suggested that the spawning ground indices developed and estimated for Pacific saury in this study might also have important applications for understanding the dynamics of a range of pelagic species residing in the Kuroshio Current ecosystem.

5. Conclusions

Three sets of spawning ground indices, uniquely reflecting different aspects of the Pacific saury spawning ground, showed significant correlations and synchronous regime shifts with CPUE and catch of Pacific saury. The regime shifts in climatic indices, spawning ground indices, and catch and CPUE of Pacific saury were detected in 1976/77, 1987/88, 1997/98 and likely in the early 2010s. The WSST in the Kuroshio region was largely affected by MOI and SOI. We infer that the impacts of variations in climatic indices and SST in the subtropical Kuroshio waters on the abundance of Pacific saury may be attributable to the altered optimal position and size of spawning grounds resulting in altered marine physicochemical properties and food availability in the early life stages of Pacific saury, which subsequently affects their mortality rates and recruitment strengths. Together, these three spawning ground indices appear to constitute a useful framework for rationalizing variations in abundance of Pacific saury, including the dramatic declines in catches during the early 1960s as well as in very recent years.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2018.12.007.

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